

# Stochastic Dynamic Population Model for Northern Corn Rootworm (Coleoptera: Chrysomelidae)

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**ABSTRACT** A stochastic dynamic population model for the complete life cycle of northern corn rootworm, *Diabrotica barberi* Smith & Lawrence, is described. Adult population dynamics from emergence to oviposition are based on a published single-season model for which temperature-dependent development and age-dependent advancement determine adult population dynamics and oviposition. Randomly generated daily temperatures make this model component stochastic. Stochastic hatch is  $50 \pm 8\%$ . A stochastic nonlinear density-dependent larval survival model is estimated using field data from artificial infestation experiments. A regional model of corn phenology is estimated to incorporate the effect of dispersal on adult mortality. Random daily weather is generated using parameters for Brookings, SD. Model performance is evaluated with deterministic simulations, which show that the population converges to zero unless adult mortality is reduced by the availability of corn pollen from the regional model of corn phenology. Stochastic model performance is evaluated with stochastic daily weather, egg hatch, and larval survival in various combinations. Sensitivity analysis is conducted to evaluate model responsiveness to each parameter. Model results are generally consistent with published data.

**KEY WORDS** *Diabrotica barberi*, *Diabrotica virgifera virgifera*, corn rootworm, adult mortality, dispersal, larval survival

CORN ROOTWORM IS the most damaging insect pest complex of corn in the United States, causing an estimated expense of \$1 billion in lost yields and control expenditures annually (Metcalf 1986). Northern corn rootworm, *Diabrotica barberi* Smith & Lawrence, and western corn rootworm, *Diabrotica virgifera virgifera* LeConte, are the species of economic concern in the primary corn growing regions of the United States. Throughout the region the western corn rootworm is generally the more problematic species, but the northern corn rootworm persists and in some areas it predominates.

Recent developments have renewed interest in corn rootworm population models. Both northern and western corn rootworm have adapted to common corn rotations to become problems even in first-year corn and the prevalence of this adaptation is spreading (Krysan et al. 1984, Levine and Oloumi-Sadeghi 1996, Onstad et al. 1999). Seed companies are currently field testing transgenic corn resistant to corn rootworm, and resistance management strategies will be part of the registration process (Information Systems for Biotechnology 1999). Rotational resistance and transgenics need to be incorporated into integrated pest management (IPM) programs. Scientific, policy, and

economic questions arising from these and similar developments can be addressed with corn rootworm population models.

Mooney and Turpin (1976) created a full life cycle model for corn rootworm, but did not differentiate between northern and western corn rootworm. Hein and Tollefson (1987) and Elliot and Hein (1991) developed single season models for western corn rootworm, and Naranjo and Sawyer (1989a) created a single season model for northern corn rootworm. These single season models were estimated and calibrated with observed air and soil temperatures from only a few years and have not been evaluated under the wide variety of weather conditions possible at the locations for which they were parameterized, except via sensitivity analysis. We are unaware of any stochastic multiple season model for either the western or northern rootworm. This study had three objectives: (1) develop a multiple season model of northern corn rootworm population dynamics, (2) make this model stochastic, and (3) evaluate model performance.

## Materials and Methods

**Daily Weather Generation.** Generated daily air and soil temperatures are used to determine emergence and drive temperature-dependent development of adults and oviposition. Daily air temperature generation is based on the method of Richardson (1981), and soil temperature generation is based on a modification of the method of Potter and Williams (1994). Mitchell

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(1999) provides a complete description of the estimation of eight Fourier series and various correlation coefficients and reports parameters for Brookings, SD (44° 18' N, 96° 48' W). The final result is a system for generating random daily weather such that the daily mean and standard deviation of maximum and minimum temperatures exhibit the same seasonal cyclic variations and correlations as observed weather. To generate deterministic weather, maximum and minimum air temperatures are set to their respective daily means, which follow seasonal cycles according to estimated Fourier series.

**Adult Population Dynamics and Oviposition.** The single season model of Naranjo and Sawyer (1989a) serves as the model of adult population dynamics from emergence to oviposition. The multiple cohort model uses daily temperatures to determine cohort development and a distribution function to determine population advancement. Temperature determines daily oviposition of mature female cohorts in an analogous manner. The model is unchanged except that a half-day time step is used instead of a one-day time step as in Naranjo and Sawyer (1989a). Mitchell and Riedell (2000) describe the model as implemented. The model predicts total oviposition (eggs per square meter) at the end of each season. Besides daily air and soil temperatures and parameters estimated by Naranjo and Sawyer (1989a), the model requires (1) the total number of emerging adults per square meter, (2) the Julian day of corn planting, and (3) the Julian day of peak corn pollination.

Naranjo and Sawyer (1989a) develop a model of adult dispersal using the difference between predictions and field observations. Because they assume that the age and reproductive status of any immigrating population is distributed evenly among native population cohorts, they note that their model does not permit generalization over space and time (Naranjo and Sawyer 1989, p. 178). Data were not available to develop a spatial model, so dispersal is not explicitly modeled. Rather, its effect on adult mortality is incorporated by means of a regional corn phenology model.

**Adult Mortality and Regional Corn Phenology.** Naranjo and Sawyer (1989a) estimated the daily proportional rate of mortality ( $M$ ) as a function of corn phenology:  $M = M_m \exp(-k\phi_f)$ , where  $\phi_f$  is the proportion of plants in a field that are flowering,  $M_m = 0.143$  is the maximum proportional rate of mortality, and  $k = 1.924$  determines the rate of decline in mortality as  $\phi_f$  increases. Under natural conditions, adults generally do not remain exclusively in their field of emergence, but disperse to neighboring fields, especially when the availability of pollinating corn decreases (Cinereski and Chiang 1968). To capture the effect of dispersal on adult mortality, we adapt Naranjo and Sawyer's (1989a) mortality model to include the regional availability of pollinating corn.

In the model, adults remain in their field of emergence until the proportion of plants in flower begins to decline. Once the proportion of flowering plants in the field of emergence is less than the proportion of

**Table 1.** Regression parameter estimates for the percentage of South Dakota corn acres silking as a function of growing degree-days accumulated from 1 May in Brookings, SD

Parameter	Estimate	SE	<i>t</i>	<i>P</i>
$a_0$	-3.13	0.587	-5.33	<0.0001
$a_1$	5.35	1.122	4.77	<0.0001
$a_2$	-1.72	0.528	-3.26	0.00196

$n = 56$ ;  $R^2 = 0.794$ ;  $F = 101.99$ ;  $df = 2, 53$ ;  $P < 0.0001$ .

plants flowering in other fields, adults move to those fields so that daily rate of mortality depends on the availability of pollinating corn in those fields. Naranjo and Sawyer's (1989a) corn phenology model is used for the proportion of plants flowering in the field of emergence, but we develop a regional corn phenology model for the availability of pollinating corn in other fields.

The National Agricultural Statistical Service in the U.S. Department of Agriculture (USDA-NASS) makes data files from the Weekly Crop Progress and Conditions Report available for downloading (USDA-NASS 2000a). Data were available for South Dakota for 1985 through 1997. These data include observations of the percentage of acres in a state that are silking or have silked on a given Julian day. This reported percentage is the average across all reporting counties, weighted by each county's planted acres in the previous year. Because most of the corn acreage in South Dakota is in the eastern third of the state where Brookings is centrally located, these state data are representative of the progression of corn silking around Brookings (USDA-NASS 2000b). Flowering as used by Naranjo and Sawyer (1989a) is equivalent to silking as used by USDA-NASS and the R1 stage as defined by Ritchie et al. (1997).

Daily maximum and minimum temperatures for Brookings, SD, for 1985 through 1997 were obtained from the National Climate Data Center (2000). Corn growing degree-days, calculated using the rectangle technique with minimum and maximum temperatures of 10 and 30°C, respectively (Higley et al. 1986), were accumulated from 1 May, the approximate earliest day that corn planting begins in South Dakota. Cumulative growing degree-days were determined for each Julian day that the percentage of corn acres silking was reported.

Various nonlinear models were fit to estimate the proportion of corn acres silking as a function of corn growing degree-days in Brookings. A quadratic function provided the best fit:  $S = a_0 + a_1G + a_2G^2$ , where  $S$  is the proportion of corn acres silking and  $G$  is corn growing degree-days in Brookings accumulated from 1 May and normalized by dividing by 760, the mean of the data used for estimation. Table 1 reports regression parameter estimates and Fig. 1 illustrates the model fit. Given the central location of Brookings in the corn-growing area of South Dakota,  $S$  is a reasonable approximation of the progression of corn silking around Brookings as a function of daily temperatures in Brookings.

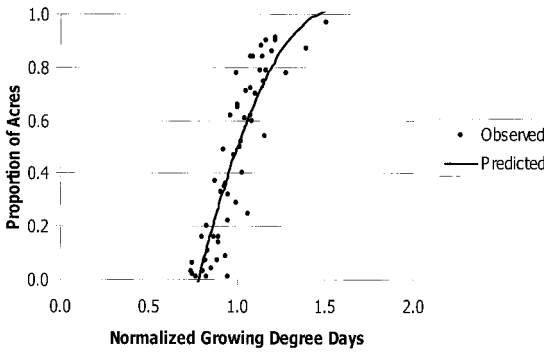


Fig. 1. Observed and predicted proportion of corn acres silking in South Dakota versus normalized corn growing degree-days in Brookings, SD

In Naranjo and Sawyer's (1989a) model, adult mortality depends on the proportion of plants in a field in flower, not  $S$ , the proportion of corn acres silking. As a result, a simplified version of Naranjo and Sawyer's (1989a) model of within-field corn phenology is embedded in the regional model of corn silking. Daily observations of the proportion of a field in flower were generated with their model of corn phenology, using deterministic daily weather and a typical plant day and day of peak flowering (20 May and 13 August). Fig. 2 (dashed line) shows the output, which is typical in terms of height and spread for other plant days and days of peak flowering. Because the tails represent insignificant proportions of corn flowering, all days with  $<20\%$  of corn flowering were dropped. The first observation was denoted Julian day  $j = \text{one}$  and the quadratic model  $\phi = b_0 + b_1j = b_2j^2$  was estimated, where  $\phi$  is the proportion of the field in flower. Table 2 reports parameter estimates.

The availability of pollinating corn in a region increases as the earliest fields in the area begin silking, remains at a plateau as fields throughout the region

Table 2. Regression parameter estimates for simulated proportion of a corn field in flower in Brookings, SD, as a function of the days after flowering begins

Parameter	Estimate	SE	<i>t</i>	<i>P</i>
$b_0$	0.112	0.0191	5.84	$<0.00001$
$b_1$	0.121	0.00304	39.7	$<0.00001$
$b_2$	-0.00427	0.000102	42.0	$<0.00001$

$n = 28$ ;  $R^2 = 0.986$ ;  $F = 892.09$ ;  $df = 2, 25$ ;  $P < 0.0001$ .

pollinate, then declines as the latest fields in the area finish pollinating. We model this progression as a spline function with specific Julian days marking changes in the regional availability of pollinating corn. Let  $j_{p0}$  denote the Julian day on which  $S$  first equals or exceeds the proportion  $p_0$ , and  $j_{p1}$  denote the Julian day on which  $S$  first equals or exceeds the proportion  $p_1$ . For the base model we use  $p_0 = 0.05$  and  $p_1 = 0.95$ . Let  $j^*$  denote the Julian day on which  $\phi = b_0 + b_1j + b_2j^2$  reaches its maximum. Setting the first derivative equal to zero and solving for  $j$  gives  $j^* = -b_1/2b_2$ . For the parameter estimates in Table 2,  $j^* = 14.2$ , so that it takes about 2 wk from the beginning of pollination for the proportion in flower to peak, and about 4 wk ( $2j^*$ ) for a field to completely pollinate. Lastly, let  $j_c$  denote the current Julian day.

Use  $\phi_o$  to denote the proportion of pollinating plants in other fields. For the model here, beginning on Julian day  $j_{p0}$ ,  $\phi_o$  begins to increase from zero according to  $\phi_o = b_0 + b_1(j_c - j_{p0}) + b_2(j_c - j_{p0})^2$ . This continues until Julian day  $j_{p0} + j^*$ , when  $\phi_o$  reaches its maximum value at  $\phi_o = b_0 + b_1(j_c - j^*) + b_2(j_c - j^*)^2$ . It remains at this maximum until Julian day  $j_{p1} + j^*$ , when it begins to decline according to  $\phi_o = b_0 + b_1(j_c - j_{p1}) + b_2(j_c - j_{p1})^2$  until it equals zero on Julian day  $j_{p1} + 2j^*$ . Fig. 2 illustrates the spline function describing the seasonal progression of  $\phi_o$  with deterministic weather (solid line), as well as the underlying quadratic equations for early

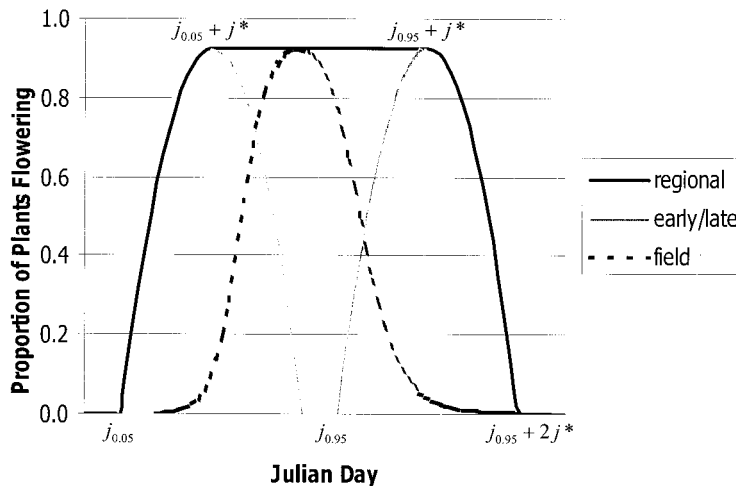


Fig. 2. Regional proportion of corn plants flowering (solid line), fitted proportion of corn plant flowering in early and late planted fields (gray lines), and proportion of corn planted flowering in a typical field (dashed line) versus Julian day.

and late fields determining the initial rise and final decline of  $\phi_o$  (gray lines).

The daily proportional rate of adult mortality is determined by adapting Naranjo and Sawyer's (1989a) model. Adult mortality  $M = M_m \exp(-k\phi_f)$  until  $\phi_f$ , the proportion of plants flowering in the field of emergence, begins to decline as silking progresses in the field of emergence. At this time, adult mortality depends on  $\phi_o$ . To account for the additional mortality resulting from adults having to search for flowering fields,  $\phi_o$  is deflated by the factor  $\delta \in [0,1]$ . When  $\phi_f \leq \delta\phi_o$ , pollinating corn in other fields provides more food so that adult mortality  $M = M_m \exp(-k\delta\phi_o)$ . In this adapted model, adults move to wherever the best food is available, but "pay" a search cost to find other pollinating corn when their field of emergence begins to complete pollinating. For the base model we use  $\delta = 1$  so that the search cost is zero, then use sensitivity analysis to examine the importance of this cost.

**Hatch.** Woodson and Ellsbury (1994) use laboratory experiments to develop a model of egg mortality as a function of the constant temperature of exposure and the duration of exposure. Woodson et al. (1996) estimate a model of egg development under varying temperatures, but do not include mortality. These were the only models of northern corn rootworm hatch found in the literature and unfortunately were not suitable for use here. As a result, a simple model of egg hatch is used. The percentage of the previous year's eggs that hatch is normally distributed with mean  $\mu_h = 0.5$  and standard deviation  $\sigma_h = 0.08$  (i.e.,  $50 \pm 8\%$ ), implying that almost 99% of the time the percentage hatch is between 30 and 70%. As with Naranjo and Sawyer's (1989a) original model, this model does not include extended diapause (Krysan et al. 1984).

For comparison with published data on northern corn rootworm hatch, Woodson and Ellsbury (1994) report hatch rates from 5 to 68% for eggs exposed up to 16 wk to different constant temperature treatments between 0 and  $-10^\circ\text{C}$  in the laboratory. Woodson et al. (1996) report average hatch rates of 56–81% in the laboratory for eggs collected from feral females near Brookings and chilled at  $8^\circ\text{C}$  for 6–9 mo.

**Larval Survival.** The model of Woodson and Jackson (1996) of northern corn rootworm larval development does not account for mortality. Woodson (1994) studied density-dependent survival of northern and western corn rootworm larvae to emergence and demonstrated that northern corn rootworm larval survival is significantly lower than western corn rootworm larvae under the same conditions. However, the reported model did not seem applicable here as it concerned the impact of interspecific competition on larval survival in potted plant experiments.

Because data for northern corn rootworm were not available, emergence data from artificial infestation field experiments with western corn rootworm are used to develop a larval survival model. However, no data were available to adjust the model for northern corn rootworm. As a result, sensitivity analysis is used

**Table 3.** Maximum likelihood parameter estimates for the conditional beta density function for larval survival

Parameter	Estimate	SE	<i>t</i>	<i>P</i>
$\alpha$	2.93	0.609	4.80	<0.001
$\omega_0$	18.3	8.07	2.27	0.023
$\omega_1$	0.0267	0.00838	3.19	<0.001

$n = 72$ .

to capture the impact of adjusting for northern corn rootworm.

Emergence data from 3 yr of artificial infestation experiments conducted near Brookings, SD are used to estimate a stochastic density-dependent larval survival function. See Riedell et al. (1996) for a complete description of the experiment. Western corn rootworm eggs were placed in the soil following the method of Sutter and Branson (1986) to obtain experimentally controlled populations of 1,200, 2,400, and 4,800 viable eggs per meter of row. Using reported plant and row spacing, these densities were converted to 1,053, 2,105, and 4,211 viable eggs per square meter. We assume that these viable eggs hatched to establish the indicated initial larval populations.

Histograms indicated that for a fixed initial larval population the proportion of western corn rootworm larvae surviving is not normally distributed about the mean, nor is the variance constant. As a result, ordinary least squares regression of survival on larval population for a linear or nonlinear specification is not appropriate. Instead of attempting to find a variance-stabilizing transformation and a nonlinear specification, maximum likelihood with a non-normal error specification is used.

The beta distribution is sufficiently flexible to be symmetric or skewed when unimodal; can be U, L, or J-shaped; and in standard form it has lower and upper bounds of 0.0 and 1.0 (Evans et al. 1993). As a result, the beta density seems appropriate because the proportion surviving must be between 0.0 and 1.0 and histograms showed varying degrees of skewness. The beta density has two shape parameters,  $\alpha$  and  $\omega$ . To capture the effect of population density on larval survival, the parameter  $\omega$  is estimated as a linear function of the initial larval population  $L$ :  $\omega = \omega_0 + \omega_1 L$ . Maximum likelihood parameters values reported in Table 3 were estimated using the ML procedure in TSP version 4.4 (TSP International 1997).

A beta density with parameters  $\alpha$  and  $\omega = \omega_0 + \omega_1 L$  has mean  $\alpha / (\alpha + \omega_0 + \omega_1 L)$  and variance  $\alpha(\omega_0 + \omega_1 L) / ((\alpha + \omega_0 + \omega_1 L)^2 (\alpha + \omega_0 + \omega_1 L + 1))$  (Evans et al. 1993). Fig. 3 plots the observed and predicted mean and standard deviation for each initial larval population to illustrate that the model fits the data well. With this model, larval survival can be deterministic or stochastic. For the deterministic case, the proportion surviving to emergence is the mean of the beta density as a function of the initial larval population. For the stochastic case, the initial larval population determines the parameters of the beta density function describing larval survival.

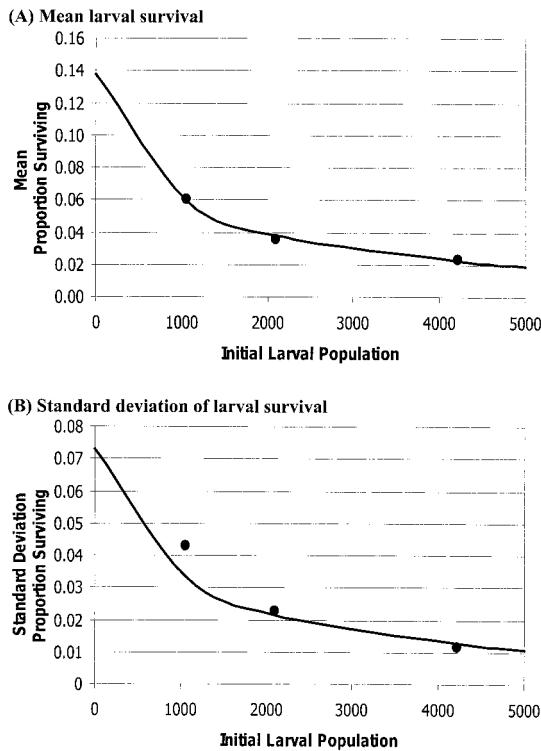


Fig. 3. Observed (dots) and estimated (line) mean larval survival to emergence versus initial larval population per square meter (A). Observed (dots) and estimated (line) standard deviation of larval survival versus initial larval population per square meter (B).

**Simulations.** The model is programmed in C++ using Microsoft's Visual C++ compiler version 5.0 (Microsoft 1997) and all simulations were conducted on a PC with an AMD-K6 550 MHz processor. In addition to parameter values as previously described, a simulation run requires specifying the Julian day of planting and day of peak flowering, as well as the initial number of eggs. The deterministic model uses deterministic daily weather for adult dynamics and oviposition, a constant percentage hatch, and the mean density-dependent larval survival model. Deterministic simulations quickly converged to their respective equilibria regardless of the initial egg population, so output at the end of 50 simulated years is used for analysis of model performance.

Stochastic versions of the model use random weather, hatch, and larval survival in various combinations and begin with an initial egg population of 1,000/m<sup>2</sup>. A common problem with stochastic population models is that there is some probability that the population will be zero. As a result, extinction eventually occurs if enough simulations are conducted, and the population can never recover without modeling recolonization. Extinctions occurred for this model, and because dispersal is not modeled, no mechanism exists in the model for population recovery. As a result, simulations were conducted in 500-yr blocks and an-

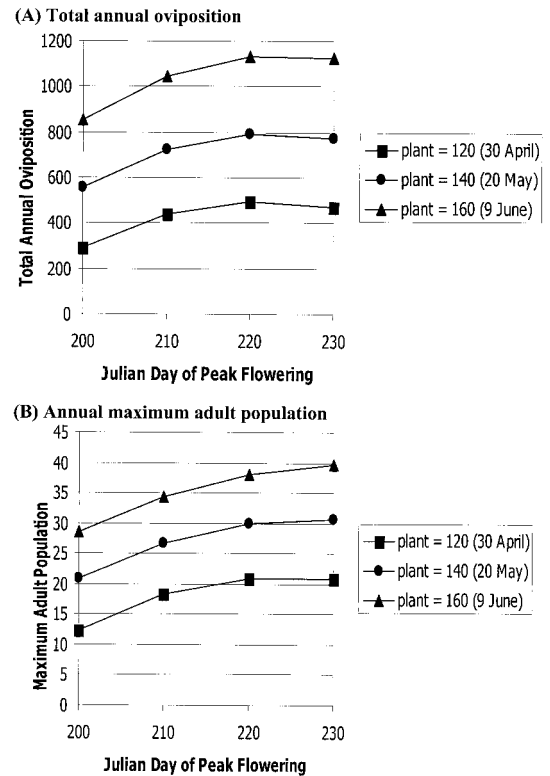


Fig. 4. Impact of plant day and day of peak flowering on simulated total annual oviposition per square meter (A) and annual maximum adult population per square meter (B) for the deterministic model.

nual output from a block was retained only if the population did not become extinct. Experimentation indicated that 10,000 simulated years of output were sufficient for the mean and the standard deviation to stabilize.

## Results and Discussion

**Deterministic Model.** All populations quickly converged to zero for the deterministic model when adult mortality depends exclusively on the availability of pollinating corn in the field of emergence. This result occurred for all reasonable choices of plant day and day of peak flowering regardless of the initial number of eggs, even if the percentage hatch was set as high as 75%. Once the effect of dispersal on adult mortality is included via the adapted adult mortality model, the population model no longer converges to zero. Fig. 4 illustrates the impact of the plant day and day of peak flowering on the predicted total annual oviposition per square meter and annual maximum adult population per square meter.

Northern corn rootworm are limited by temperature and availability of food (Naranjo and Sawyer 1987), which the model captures with temperature-dependent development and corn pollen availability



determining mortality. As a result, when adults in the model are limited to their field of emergence, gravid females develop too slowly relative to their food supply to complete development and lay sufficient eggs to generate a sustainable population. If mortality also depends on regional corn phenology so that food availability more accurately reflects field conditions, gravid females can complete development and oviposit sufficient eggs to maintain a viable population. Furthermore, because the population is also limited by temperature, as the plant day and day of peak flowering increase, the predicted total annual oviposition and annual maximum adult population increase as well (Fig. 4). These results provide support for the hypothesis that adult dispersal to neighboring fields is essential for long-term survival of the species in regions dominated by hybrid corn with synchronized flowering.

To convert simulated adult populations from beetles per square meter to the more common beetles per plant requires assuming a plant density. A density of 70,000 plants/ha implies that dividing by seven converts beetles per square meter to beetles per plant. Using this conversion factor, the model predicts that at all plant day and day of peak flowering combinations, the maximum adult density is always  $>1$  adult per plant, the IPM threshold commonly recommended for corn rootworm. As part of the sensitivity analysis mean larval survival is reduced 10 and 20% to adjust the larval survival model for northern corn rootworm. Even this adjustment does not reduce the maximum adult population below one beetle per plant. These model predictions require calibration beyond that conducted by Naranjo and Sawyer (1989a), but as they stand, they support the prophylactic treatment of continuous corn with soil insecticides. However, natural corn rootworm populations fluctuate randomly. As a result, in some years the population does not exceed the threshold and thus soil insecticide is not recommended the following year. Results from the stochastic model indicate how frequently this occurs.

The model predicts peak adult populations that are comparable to field data. Fig. 5 in Naranjo and Sawyer (1989a) indicates maximum adult populations near Ithaca of around 25 adults per square meter for an early flowering variety, and around 35 adults per square meter for a late flowering variety. Fig. 1 in Lance et al. (1989) indicates peak adult populations of  $\approx 2.5$  and five adults per plant for two locations in eastern South Dakota, or  $\approx 17.5$  and 35 adults per square meter. Mullock et al. (1995) report per plant peak adult populations for seven fields near Elora, Ontario. Two fields had 0.1, two had 0.2, and the other three fields had 0.7, 1.0, and 3.6 adults per plant.

**Stochastic Model.** All stochastic simulations are conducted using the adapted model of adult mortality; otherwise populations rapidly converge to zero. To analyze the impacts of various sources of randomness, daily weather, percentage hatch, and larval survival were made stochastic in all possible combinations. The plant day and day of peak flowering are fixed at the

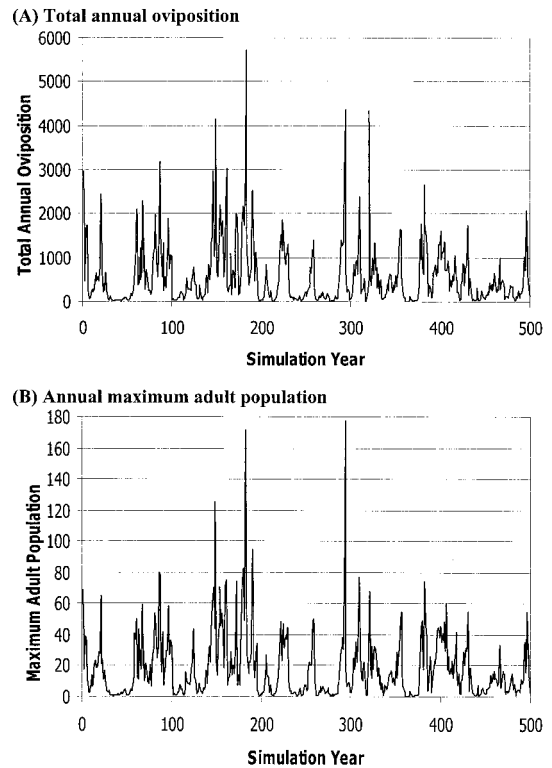


Fig. 5. Typical 500-yr time series of simulated total annual oviposition per square meter (A) and annual maximum adult population per square meter (B).

approximate averages of 140 (20 May) and 215 (3 August) for South Dakota. For comparison to deterministic results, sample means  $\pm$  SEM for total annual oviposition and annual maximum adult population are reported in Table 4 for each set of 10,000 simulations.

Stochastic hatch has no effect on the mean of either total annual oviposition or maximum annual adult population and only increases the standard deviation of each. This occurs because as it is modeled, hatch becomes stochastic by adding a mean zero random error. Because there is no nonlinearity introduced by stochastic hatch, it merely increases the variability of oviposition and the adult population.

Using random daily weather increases average oviposition by 33% and the average adult population by 15%. Random weather has this impact because several aspects of the northern corn rootworm population dynamics are nonlinear functions of daily temperature. For example, the function describing the rate of development for reproducing adults is convex over the range of typical temperatures (Figure 4 in Naranjo and Sawyer 1988). As a result, the average rate of development with varying temperatures will be greater than the rate of development when the temperature is held constant at its mean. This occurs because when temperatures are above the mean, adult development increases more than proportionally and when the tem-

**Table 4.** Impact of stochastic factors on simulated total annual oviposition per square meter, annual maximum adult population per square meter, and frequency (%) that maximum adult population exceeds one beetle per plant

Hatch	Stochastic factors		Total annual oviposition	Annual maximum adult population	Frequency adult population > 1 beetle per plant
	Larval survival	Weather	Mean $\pm$ SEM	Mean $\pm$ SEM	
X			770.7 $\pm$ 208.5	28.1 $\pm$ 5.6	99.8
	X		489.6 $\pm$ 472.6	18.2 $\pm$ 17.6	69.9
		X	1,030.1 $\pm$ 495.1	32.8 $\pm$ 10.8	97.9
X	X		437.0 $\pm$ 443.8	16.2 $\pm$ 16.5	64.9
X		X	1,011.0 $\pm$ 508.4	32.1 $\pm$ 11.4	97.9
	X	X	688.2 $\pm$ 762.2	21.9 $\pm$ 21.5	73.6
X	X	X	670.6 $\pm$ 735.3	21.4 $\pm$ 21.3	72.7
			770.0 $\pm$ —	28.6 $\pm$ —	100.0

$n = 10,000$ ; plant day = 140 (20 May); day of peak flowering = 215 (3 August). X indicates that a factor is stochastic; — indicates that it is deterministic.

peratures are below the mean, adult development decreases less than proportionally.

The rate of adult development is just one of several nonlinear functions of daily temperatures in the model. A priori determining the net effect of all these functions on total annual oviposition and the maximum adult population is difficult and must be done with model simulations. Because using random daily weather causes an increase in the mean of both population measures relative to deterministic results reported in Table 4, the combined result is that both are convex in temperature.

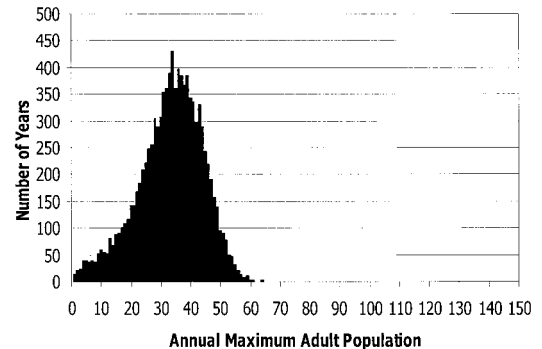
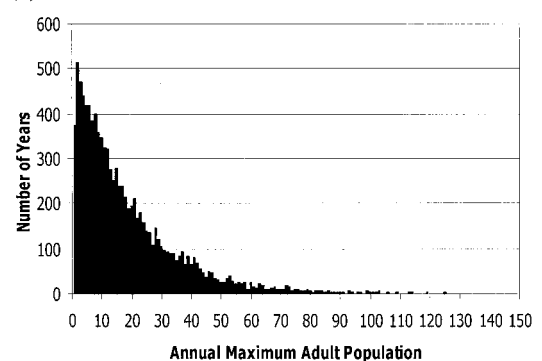
Using random larval survival has the opposite effect—it decreases average oviposition and the average adult population both by 36%. This result occurs because of a nonlinear function as well. The proportion of larvae surviving is convex in the initial larval population (Fig. 3). However, the number of larvae surviving is concave in the initial larval population—as the initial larval population increases, the number surviving to emergence increases as well, but at a decreasing rate. As a result, the average number of larvae surviving to emergence will be less than the number surviving to emergence when the initial larval population is fixed at its mean. This occurs because when the initial larval population is higher than average, the number surviving to emergence increases less than proportionally and when the initial larval population is lower than average, the number surviving to emergence decreases more than proportionally.

Because the model is nonlinear, average oviposition and adult population when there are random variables do not equal oviposition and the adult population when random variables are fixed at their means. The net effect when both daily weather and larval survival are random cannot be predicted a priori, but results in Table 4 show that mean oviposition and mean adult population decrease 13 and 25%, respectively. Random hatch has little effect on these means.

Examining the SEM indicates that they are particularly large relative to the means when larval survival is stochastic. This wide variation is evident in a time series plot of total annual oviposition and the maximum adult population (Fig. 5) for a typical 500-yr simulation with stochastic hatch, larval survival, and

weather. The fluctuations are qualitatively consistent with the large population differences observed between fields (Mullock et al. 1995) and within fields (Ellsbury et al. 1998).

Plotting histograms of oviposition and adult populations provides an indication of their respective probability distributions and makes differences in distributions apparent. Fig. 6 shows histograms for the data used to create Table 4 for the cases when weather alone is stochastic and when larval survival alone is

**(A) Stochastic weather****(B) Stochastic larval survival**

**Fig. 6.** Histogram of simulated annual maximum adult population per square meter when weather alone is stochastic (A) and larval survival alone is stochastic (B). Histograms for oviposition have similar shapes.

stochastic. These histograms illustrate the two shapes that occur. Stochastic weather creates a skewed unimodal distribution, while stochastic larval survival creates a smooth L-shaped distribution. When weather and larval survival are both stochastic, the resulting histogram has the same smooth L-shape as when larval survival alone is stochastic, but is more spread out because of the greater variance. The impact of stochastic larval survival dominates the impact of stochastic weather, as occurs with mean oviposition and adult populations when these factors are stochastic.

Figures 7 and 8 in Ellsbury et al. (1998) present field maps of site-specific populations of emerging northern corn rootworm adults that are qualitatively consistent with the histogram shape when all factors are stochastic. Most areas of the fields have very low to no emerging northern corn rootworm adults, while a few areas have high populations. Though they report no histograms, the shape of such histograms should be similar to those reported in Fig. 6 here.

When hatch alone is stochastic, it creates a symmetric unimodal distribution that appears normal (not shown). This occurs because as it is modeled, stochastic hatch is created by adding a mean zero normal random error. When stochastic hatch is used in combination with other stochastic factors, it has little impact on the shape of the histograms (not shown), but affects the SEM as reported in Table 4.

Converting the annual adult population to a per plant basis by dividing by seven allows determination of how often the adult population rises above the commonly recommended IPM threshold of one adult per plant. These frequencies are reported as percentages in the last column of Table 4. Only when larval survival is stochastic does the adult population fall below the threshold with any substantial frequency. Assuming these results are accurate, a farmer using this threshold would treat with soil insecticides on average  $\approx 75\%$  of the years. The deterministic model predicted that the pest population would always remain above the treatment threshold and simulations with stochastic hatch and/or weather do not deviate substantially from this.

This interpretation of the results reported in Table 4 is misleading because the effect on population dynamics of soil insecticide applications or other management methods is not incorporated. Extensions of the model include yield loss and a management decision models to analyze the economics of corn rootworm IPM. However, the impact of continuous soil insecticide applications can be simulated. Reducing larval survival by 50% represents an estimate of the impact that annual soil insecticide applications has on larval survival. Imposing this 50% reduction causes populations to rapidly converge to zero in deterministic and stochastic simulations. This result supports attempts to manage northern corn rootworm populations regionally, such as the USDA Corn Rootworm Areawide Management project currently in progress. However, note that this model does not incorporate recolonization by dispersing adults.

**Table 5.** Percentage change in total annual oviposition per square meter and annual maximum adult population per square meter with a  $\pm 10\%$  parameter change in the deterministic model

Parameter	Total annual oviposition		Annual maximum adult population	
	-10%	+10%	-10%	+10%
Regional phenology				
$a_0$	180.5	-100.0	75.4	-100.0
$a_1$	172.9	-100.0	70.3	-100.0
$a_2$	181.5	-100.0	76.4	-100.0
$b_0$	-1.5	1.5	-1.1	1.0
$b_1$	-32.3	36.5	-24.5	22.6
$b_2$	-25.1	32.2	-18.5	19.8
$p_0$	0	0	0	0
$p_1$	-76.9	182.0	-69.3	77.0
$\delta$	-34.9	34.8	-32.7	32.4
Hatch				
$\mu_h$	-23.0	18.8	-23.0	18.8
$\sigma_h$	0.0	0.0	0.0	0.0
Larval survival				
$\alpha$	-27.9	27.8	-27.9	27.8
$\omega_0$	17.8	-17.8	17.8	-17.8
$\omega_1$	11.1	-9.1	11.1	-9.1

**Sensitivity Analysis.** Naranjo and Sawyer (1989b) conducted extensive sensitivity analysis of their model, which is not repeated here. Sensitivity analysis here involved changing each parameter individually  $\pm 10\%$  to determine the resulting impact on oviposition and the adult population. Results are summarized in Table 5 for the deterministic model. Conducting sensitivity analysis for the stochastic model gives differences between deterministic and stochastic results similar to those in Table 4.

Model results are extremely sensitive to the model of regional corn phenology, as evidenced by the large percentage changes in oviposition and adult populations for 10% changes in the parameters  $a_0$ ,  $a_1$ , and  $a_2$ . Any increase in these three parameters accelerates regional corn development so that flowering begins and ends earlier in the season. This shortens the duration of corn pollen availability and shifts it to earlier in the season when temperatures are generally cooler. In Fig. 2 this decreases the width of the curve determining the regional proportion of corn plants in flower and shifts it left. As a result, adults develop too slowly relative to their food supply to complete development and lay sufficient eggs to generate a sustainable population. Decreasing any of these three parameters has the opposite effect.

The sensitivity of oviposition and adult populations to the parameters  $b_0$ ,  $b_1$  and  $b_2$  occurs for similar reasons, but their effects are not as extreme. These parameters determine the slopes of the ends of the curve describing the regional proportion of corn plants in flower and its height, not its overall duration or location in the season (Fig. 2). Decreasing  $b_1$  or  $b_2$  causes the height of the curve to decrease and both ends to rise and fall more rapidly. As a result, daily mortality throughout the season increases due to the height decrease and the end of season mortality increases due to the more rapid decline in food avail-



ability. The reverse is true when  $b_1$  or  $b_2$  are increased. Increasing and decreasing  $b_0$  has little effect on the height of the curve or the shape of its ends, and so model results are relatively insensitive to  $b_0$ .

The parameter  $p_0$  determines how early in the season other fields begin flowering, which in Fig. 2 corresponds to moving the beginning of the curve by changing  $j_{p0}$ . However, early in the season adults have sufficient food in their field of emergence so that changing  $p_0$  does not affect population dynamics. Conversely,  $p_1$  determines the availability of pollinating corn late in the season, which in Fig. 2 corresponds to moving the end of the curve by changing  $j_{p1}$ . Increasing  $p_1$  allows adults to survive longer and oviposit more, so that both the maximum adult population and annual total oviposition increase. Similarly,  $\delta$  determines the cost, in terms of increased or decreased mortality, of dispersing from the field of emergence to search for pollinating corn. Decreasing  $\delta$  increases this cost and hence adult mortality, so that both the maximum adult population and annual total oviposition decrease. Increasing  $\delta$  causes the opposite. The large percentage changes resulting from changing  $p_1$  and  $\delta$  indicate that the model is very sensitive to these parameters and hence to the modeling of the effect of dispersal on adult mortality.

Changing larval survival parameters changes both the mean and standard deviation of larval survival, but because the deterministic model is used, only changes in the mean matter for results reported in Table 5. Increasing  $\alpha$  increases mean larval survival, particularly at lower initial larval populations. As a result, mean oviposition and adult populations increase substantially because initial larval populations are more likely to be low given the shape of the oviposition histogram (Fig. 6). Increasing  $\omega_0$  decreases mean larval survival, particularly at lower initial larval populations, and so has the opposite effect. Increasing  $\omega_1$  also decreases mean larval survival, but more at higher initial larval populations, and so has the same effect as increasing  $\omega_0$ . However, because initial larval populations are less likely to be at higher levels, the effect is smaller.

In laboratory potted plant experiments, Woodson (1994) reported lower density-dependent survival for northern corn rootworm exposed to the same conditions as western corn rootworm. The larval survival model developed here was estimated with field data from artificial infestation experiments with western corn rootworm. As a result, simulations reducing mean larval survival 10 and 20% are conducted to analyze the probable impact of adjusting the larval survival model to fit northern corn rootworm. For a 10% reduction, mean oviposition and adult populations fall 30.7% and for a 20% reduction they fall 61.5%. These results and those reported in Table 5 show that model predictions are fairly sensitive to the larval survival model. Unfortunately, data were not available to develop a larval survival model for northern corn rootworm, but these results give some indication of the likely impacts this would have on model behavior.

**Model Limitations.** Model limitations include the model of egg hatch, the larval survival model estimated with western corn rootworm data, and adult dispersal. These limitations originate from the lack of data concerning these aspects of the population ecology of the northern corn rootworm. Nevertheless, sensitivity analysis for the various parameters controlling these aspects does provide some insight into the qualitative contributions of each to the population dynamics of the northern corn rootworm.

This model did not generate viable populations unless it used the modified model of adult mortality which depends on the regional availability of food. As such, this provides insight into the crucial role dispersal plays in the population dynamics of northern corn rootworm. Indeed, sensitivity analysis indicated that model results were extremely sensitive to some of the parameters because of their impact on adult mortality. However, the regional corn phenology model does not make this a spatial model. Rather, this is a model of a single patch embedded in a regional model of food availability. A spatially explicit model in which adults move in a landscape with corn fields in different stages of development is the best way to model population dynamics. However, a lack of data makes creating such a model difficult.

This stochastic dynamic northern corn rootworm population model can serve as a foundation for other studies, such as the economics of corn rootworm IPM or a feasibility analysis of corn rootworm IPM insurance. To address the development of rotational resistance for both problematic corn rootworm species and the advent of transgenic technologies with their associated concern for resistance management, a population genetics model could be added. All of these point to the fact that a better understanding of egg hatch, larval survival, and adult dispersal is required to improve our understanding of northern corn rootworm population dynamics.

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